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Availability of Drift Materials and the Covering Response of the Sea Urchin *Strongylocentrotus purpuratus* (Stimpson)[1]

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ABSTRACT: Individuals of *Strongylocentrotus purpuratus* (Stimpson) are found covered with a variety of debris. Algae and surf grass often are cover on the aboral surface and are eaten on the oral surface. *Strongylocentrotus purpuratus* individuals show no tendency to drop their cover at night and assume it again at daybreak. Individuals of this species are more extensively covered in areas of surge activity than they are in tidepools. The materials most frequently used for cover also differ in these two areas. The availability of drift materials is the most important factor in determining the extent of covering and the types of covering materials held by *Strongylocentrotus purpuratus*.

Several species of sea urchins are known to display a covering response, i.e., covering the aboral surface with stones, shell fragments, terrestrial leaves, algae, and other debris. This behavior has been described in some detail for several species of *Lytechinus* (Millott 1956, Sharp and Gray 1962, Lees and Carter 1972). Recently, Dayton, Robillard, and Paine (1970) noted this behavior in *Sterechinus neumayeri*, a sea urchin found in the Antarctic.

Many hypotheses have been proposed to explain this phenomenon. In *Lytechinus variegatus*, changes in light intensity trigger the covering response (Millott 1956). This species sheds its cover at sundown and assumes it at the onset of daylight. Sharp and Gray (1962) concluded that, in *L. variegatus*, covering materials are used as protection against intense light. However, Lees and Carter (1972), working with *Lytechinus anamesus*, suggested that covering materials stabilize the sea urchin during periods of heavy surge rather than act as a protective mechanism against ultraviolet radiation or sunlight.

Boone (1928, cited in Sharp and Gray 1962) proposed that covering by *Lytechinus variegatus* helps to prevent detection by predators and potential prey. Dayton, Robillard, and Paine (1970) showed that covering in the Antarctic sea urchin *Sterechinus neumayeri* protects it from predation by the actinarian *Urticinopsis*.

Evechinus chloroticus, a common New Zealand sea urchin, is believed to cover itself primarily when capturing food, i.e., drift algae (Dix 1970). Covering appears to be a tactile, rather than a photic, response in this species. Ebert (1968) also suggested that drift algae captured by intertidal populations of *Strongylocentrotus purpuratus* are an important source of food. Lowry and Pearse (1973) further found that subtidal populations of *S. purpuratus* feed upon drift algae when the urchins inhabit both crevices and open areas.

Populations of *S. purpuratus* found in areas of high surge activity seem to cover themselves more extensively than do those found in tidepools. In this paper I describe an investigation to test the hypothesis that this variance is due to differential availability of drift materials in the two areas.

MATERIALS AND METHODS

Field experiments and observations were carried out at two locations: at Shell Beach, a Sonoma County state park, and near Horseshoe Cove, on the biological reserve at Bodega Marine Laboratory. At Shell Beach the populations of *Strongylocentrotus purpuratus* are found in areas of high surge activity near mean lower

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low water. The populations studied near Horseshoe Cove are located in tidepools between 5 and 7 feet above mean lower low water.

Determination of Duration of Response

The intertidal populations of *S. purpuratus* that I studied were impossible to observe directly during high tides. Thus, the following experiment was carried out to discover whether the covering response in *S. purpuratus* displays diurnal periodicity, i.e., whether the cover is dropped at night and picked up again during the day, as occurs in *Lytechinus variegatus* (Sharp and Gray 1962). Stones, leaves, and shells were collected and numbered with nail polish. These items were then replaced upon sea urchins that had been previously covered with the same types of materials. Numbered stones and leaves were placed on urchins at Shell Beach; numbered shells were placed on urchins in tidepools near Horseshoe Cove. On 3 consecutive days I recorded the number of marked objects that were being held by the same sea urchins.

Measurements of Surface Area Covered

I compared the extent of covering in tidepool and in surge area populations by determining the surface area of items used as cover. Sample groups of 20 sea urchins were taken at random points in the two areas. Nine such samples were taken at Shell Beach; five at Horseshoe Cove. All the urchins in each group were stripped of their cover and then returned to their previous locations.

The materials collected in this manner were air-dried for several days and separated into seven categories: stones, shells, terrestrial leaves, wood, algae, surf grass, and miscellaneous. The dried collections were then spread out on shelf paper and painted over with spray paint. When the paint was dry and the debris had been removed, the paper looked like a "shadow picture" of the covering material. The paper was white in areas where the objects had been placed and colored in the spaces in between objects. Since the white portion corresponded to the surface area covered by the debris, all the white pieces were carefully cut out and weighed. I then compared this weight to the weight of a 1 cm square of the same paper to determine the surface area covered.

Availability of Drift Materials

To compare the relative amount of drift material available in surge areas to drift material found in tidepool areas, I made a net (diameter, 25 cm; length, 90 cm; approximately 2 mm nylon mesh) to trap the debris. I took four collections at Shell Beach and at Horseshoe Cove when the tide was 1.5 feet above mean lower low water. A collection consisted of 75 sweeps, each of 5-second duration. Each collection was made at sites where I had previously taken 20-urchin samples of covering material. The sweep collections were taken directly on or above these sites in order to collect debris that would actually be available to the same urchins that I had sampled earlier. A set of four collections was also made at Horseshoe Cove when the tide was 5.8 feet above mean lower low water. The debris netted in each collection was then air-dried overnight and weighed.

Observations were made in areas where *Strongylocentrotus purpuratus* individuals are found on vertical and horizontal surfaces. Those individuals found on vertical surfaces were always covered with lightweight objects (algae, leaves, wood); whereas, those on horizontal surfaces were covered with both lightweight and heavy objects (stones, shells). Because no heavy objects were collected in my netted drift samples, it seems plausible that heavy objects are not carried in the drift to a great extent. Rather, stones and shells may be present on the substrate and merely moved around by the surge; thus, those urchins attached on vertical surfaces would not have an opportunity to collect such items.

To test this idea, I found a large rock at Shell Beach that had both a vertical and horizontal face; the total number of sea urchins present on both faces of the rock was 99. I then stripped all the cover from these urchins to see what type of cover they took up during the next 3 days.

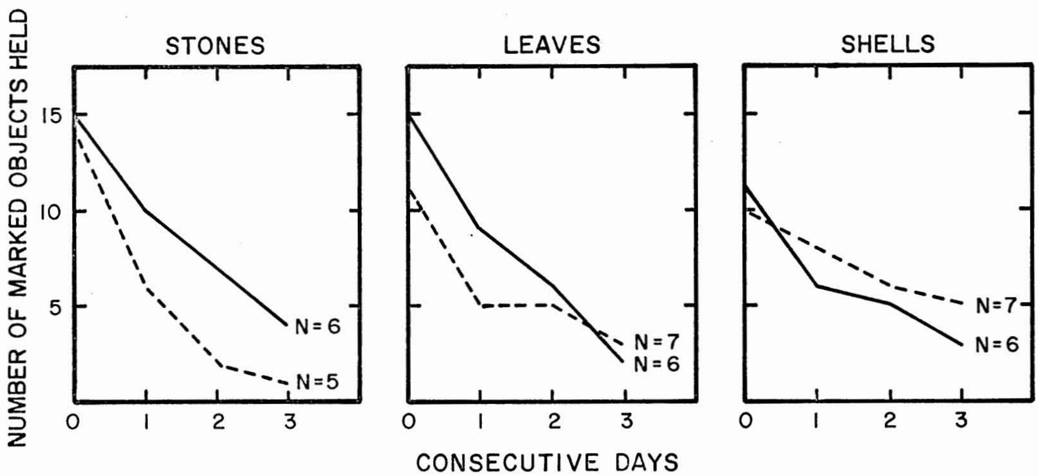

FIGURE 1. Total number of marked objects held by the same sea urchins over a 3-day time period. N = number of sea urchins in a particular observational group. Solid and dotted lines represent two different groups of urchins holding the same type of marked objects. Marked stones and leaves were on sea urchins at Shell Beach in low-lying areas of high surge activity. Marked shells were on sea urchins at Horseshoe Cove in tidepools.

RESULTS

Determination of Duration of Response

The results presented in Figure 1 indicate that *Strongylocentrotus purpuratus* does not drop its cover at night and assume it again during the day. Several individuals held the same objects for up to 3 days. During this time, the urchins also collected other debris and seemed to have replaced the cover that I had removed from them.

Measurements of Surface Area Covered

The results of the comparison between total surface areas covered in tidepool and in surge area populations are shown in Figure 2. Using the Mann-Whitney U-test (Goldstein 1964), I found that a greater (significant to 1 percent) amount of surface area is covered in the surge area than in the tidepool area.

A comparison of the coverage provided by the seven classes of materials held by the sea urchins was then made. The percentage of total coverage for each class was found for each sample (Table 1). There was no significant difference in the percentage of urchin surface covered among algae, surf grass, and miscellaneous items. However, the differences were significant (to 1 percent) between the surge area and tidepool populations with respect to the type of materials used to cover. Thus, leaves and wood made up a greater percentage of total coverage in the surge area populations; whereas, stones and shells formed a greater percentage of the total coverage in tidepool populations.

Availability of Drift Materials

The results for the series of 75 5-second sweeps are presented in Table 2. Using the Mann-Whitney U-test, I found a significantly greater (significant to 2.5 percent) amount of drift material present in the surge area as compared with that present in the tidepool area at both 1.5 and 5.8 feet above mean lower low water. There is also a greater variety of drift debris in the surge area (leaves, wood, algae, surf grass) than in the tidepool area (almost completely algae and surf grass). No heavy materials (stones or shells) were present in these collections.

The results of observations in areas where *S. purpuratus* are found on vertical and horizontal surfaces are presented in Table 3. Using the Mann-Whitney U-test, I found, for the 3-day observation period, that the number of urchins on vertical surfaces holding shells or stones was significantly less (significant to 5 percent) than was the number of urchins on horizontal surfaces holding stones or shells.

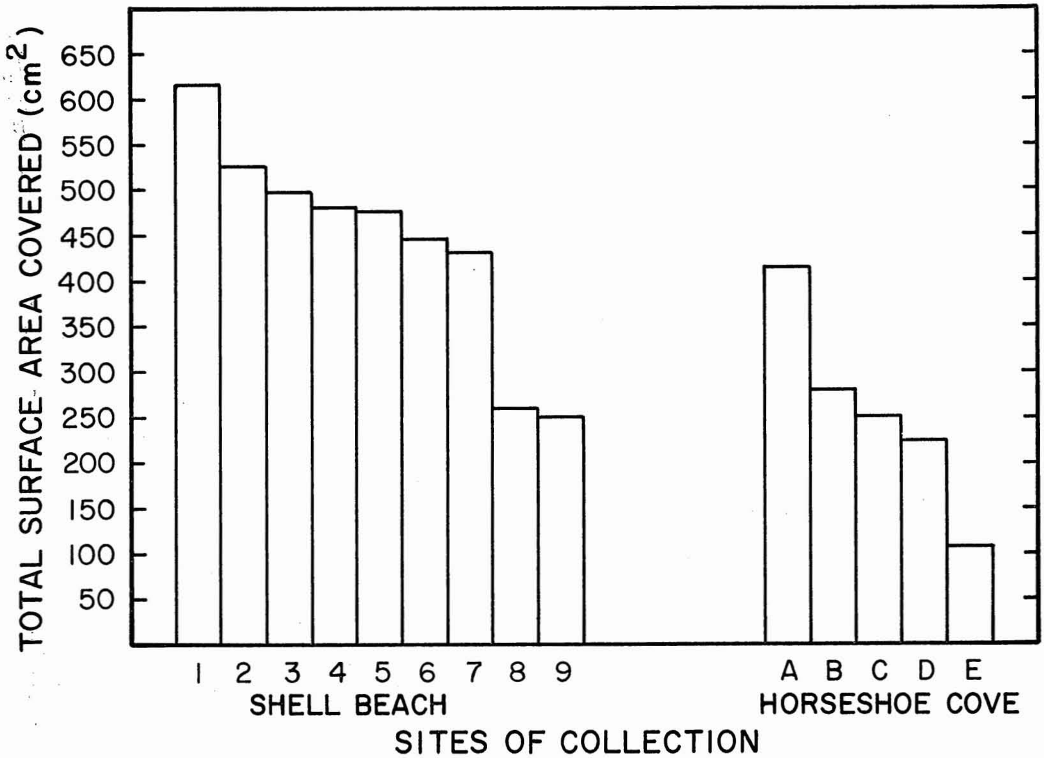

FIGURE 2. Total surface area covered per samples of 20 *Strongylocentrotus purpuratus*. Numbers 1 through 9 represent sites of collection at Shell Beach, which were in low-lying areas of high surge activity. Letters A through E represent sites of collection near Horseshoe Cove, which were in tidepools.

TABLE 1

PERCENTAGE OF TOTAL SURFACE AREA COVERED BY ALL TYPES OF COVERING MATERIAL FOR EACH SAMPLE OF 20 INDIVIDUALS OF *Strongylocentrotus purpuratus*

	COVERING MATERIALS						
SITE	STONES	SHELLS	LEAVES	WOOD	ALGAE	SURF GRASS	MISCELLANEOUS
1	0	0.47	65.02	6.66	18.87	7.08	1.90
2	0	3.97	65.22	10.31	11.49	7.02	1.98
3	4.00	15.09	62.37	6.82	6.58	2.54	2.60
4	1.74	2.68	84.08	7.18	0.49	3.64	0.20
5	0.35	3.71	83.47	5.60	0	6.03	0.84
6	1.62	10.62	68.48	7.06	4.93	7.28	0
7	15.22	8.78	53.45	4.23	11.73	5.90	0.70
8	1.08	12.25	71.95	5.86	3.20	4.09	1.57
9	0	2.33	86.32	3.63	1.01	6.31	0.41
$\bar{x}\pm1$ SD	2.67 ± 4.88	6.66 ± 5.14	71.15 ± 11.29	6.37 ± 1.93	6.48 ± 6.39	5.54 ± 1.71	1.13 ± 0.91
A	17.50	67.25	0	0.17	2.25	3.27	9.56
B	24.86	49.79	1.35	0.27	14.15	1.66	7.93
C	1.72	74.34	16.53	3.17	3.22	0	1.02
D	20.16	60.83	1.13	0	1.10	3.36	13.42
E	12.04	55.82	5.66	0.71	3.59	21.16	1.02
$\bar{x}\pm1$ SD	15.26 ± 8.87	61.61 ± 9.59	4.93 ± 6.83	0.86 ± 1.32	4.86 ± 5.28	5.89 ± 8.65	6.59 ± 5.46

NOTE: Samples 1 through 9 were taken at Shell Beach; samples A through E were taken at Horseshoe Cove.

TABLE 2

COMPARISON OF WEIGHTS AT THE TWO STUDY SITES

SITE	TIDAL HEIGHT AT TIME OF COLLECTION (feet)	DRY WEIGHT OF DRIFT MATERIAL COLLECTED (grams)
Shell Beach	1.5	
2		11.02
5		10.48
6		3.43
8		13.95
$\bar{x} \pm 1$ SD		9.72 ± 4.46
Horseshoe Cove	1.5	
A		0.18
C		0.01
D		3.40
E		0.13
$\bar{x} \pm 1$ SD		0.93 ± 1.65
Horseshoe Cove	5.8	
A		1.42
C		1.25
D		0.68
E		0.70
$\bar{x} \pm 1$ SD		1.01 ± 0.39

NOTE: Each net sample consisted of 75 5-second sweeps. Sites of collection at Shell Beach were in low-lying areas of high surge activity; sites of collection near Horseshoe Cove were in tidepools.

show that *Strongylocentrotus purpuratus* does not drop its cover at night. If this were the case, individuals most likely would not retain the same numbered objects for up to 3 days with surge constantly present. Thus, in contrast to species of *Lytechinus*, light is not a proximate factor in the covering response of *S. purpuratus*.

A comparison of the total surface area measurements of covering materials (Figure 2) shows that those urchins found in areas of high surge activity are more extensively covered than are those in tidepool regions. This may be the result of more debris being available in the surge areas. The results of my net collections support this hypothesis. Table 2 shows that there is a greater amount of drift material present in the surge areas than in the tidepools. These results are in agreement with observations made by Dix (1970) concerning the urchin *Evechinus chloroticus*. He suggested that the extent of covering by *E. chloroticus* depends mainly on the availability of covering material.

For *S. purpuratus* individuals, the type of covering materials held also seems to be determined by the availability of drift items. A greater variety of debris was found in the net collections in surge areas than was found in the net collections in tidepool areas. Surge collections included leaves, wood, surf grass, and algae; tidepool collections consisted almost totally of algae and surf grass. This would account for the greater "percentage of total

TABLE 3

COVERING MATERIALS FOUND ON A POPULATION OF *Strongylcentrotus purpuratus* LOCATED ON BOTH THE VERTICAL AND HORIZONTAL FACES OF A ROCK AT SHELL BEACH

LOCATION AND DAY OF OBSERVATION	TOTAL NUMBER OF URCHINS	NUMBER HAVING SOME COVER	NUMBER COVERED WITH LIGHTWEIGHT OBJECTS ONLY	NUMBER COVERED WITH SHELLS OR STONES
Vertical Face	58			
1		57	54	3
2		58	54	4
3		58	55	3
Horizontal Face	41			
1		41	29	12
2		41	18	23
3		41	19	22

NOTE: Observations were carried out for 3 consecutive days.

DISCUSSION

Diurnal periodicity in the covering response has been described for species of *Lytechinus* (Millott 1956, Sharp and Gray 1962, Lees and Carter 1972). Results presented in Figure 1 coverage" measurements for leaves and wood in the surge area.

Heavy objects (stones and shells) were not held by sea urchins that inhabited vertical rock surfaces. No heavy objects were found in any net collections, so perhaps they are not available to sea urchins living on vertical surfaces. Alternatively, they may be too heavy to be held firmly by the urchin at that angle.

The covering response in *S. purpuratus* can best be described as a tactile response: the urchins hold on to whatever is available. Light does not trigger the response in this species. Urchins can be found covered in crevices and shaded areas as well as in areas exposed to sunlight. Individuals of *S. purpuratus* are covered with a variety of items; the type of cover held and the extent of covering correlate with the availability of drift materials.

Covering in *S. purpuratus* is not an adaptation to stabilize the urchin in times of heavy surge, as suggested by Lees and Carter (1972) for the sea urchin *Lytechinus anamesus*. *L. anamesus* lives on a shallow, soft substrate and has little opportunity to attach itself to solid objects. However, this is not the case with *S. purpuratus*. These intertidal urchins are firmly attached to the rock substrate and some individuals make depressions in the rock, such depressions providing more area for attachment. A great deal of force is required to loosen these animals once they have fastened themselves to the rock. Neither covered nor uncovered individuals of *S. purpuratus* seem to have any problem remaining firmly attached to their substrate.

Protection from predation is an explanation for the covering response that may apply to *S. purpuratus*. Predators of *S. purpuratus* include the sea otter *Enhydra lutris*, the sea star *Pycnopodia helianthoides* (Lowry and Pearse 1973), the anemone *Anthopleura xanthogrammica* (Dayton 1973), and perhaps marine birds (J. S. Pearse, personal communication). Covering may camouflage *S. purpuratus* from the view of vertebrate predators. *Pycnopodia* is a very fast-moving sea star and covered or uncovered sea urchins cannot move quickly enough to escape from it.

The anemone *Urticinopsis* preys actively upon the sea urchin *Sterechinus neumayeri* in the Antarctic. Here covered urchins often escape from the anemone, whereas uncovered urchins are always eaten (Dayton, Robillard, and Paine 1970). Covered individuals of *S. purpuratus* may be able to escape from *A. xanthogrammica*, but this anemone does not seem to be an active predator upon *S. purpuratus*. Rather, *A. xanthogrammica* feeds on *S. purpuratus* as an indirect result of predation on the urchin by *Pycnopodia*. Dayton (1973) reported that *Pycnopodia* "stampedes" aggregations of *S. purpuratus*, and that the urchins within 5–10 cm of the sea star respond by spine and pedicellariae movement and by retreating. When there are high densities of urchins, the lack of available rock substrate usually forces the fleeing urchins to climb onto the backs of others. In this precipitous situation the urchin does not have a firm hold and is very susceptible to being removed by wave action. Dayton observed that most of these fleeing urchins are dislodged by wave action and that many are swept into *Anthopleura* patches. If the covered urchins retain their cover during their flight from *Pycnopodia* and their subsequent removal by wave action, they may have an advantage over uncovered urchins when they reach the *Anthopleura* patches.

The capture of food is probably an ultimate factor in the covering response of *S. purpuratus*. When the populations of *S. purpuratus* that I studied covered themselves with algae or surf grass, these items were often used as cover on the aboral surface and as food on the oral surface. This occurred with many types of brown and red algae (including several species of coralline red algae) as well as with surf grass. Nevertheless, *S. purpuratus* also is found utilizing nonedible items (stones, shells, terrestrial leaves) as cover. (It seems unlikely to me that terrestrial leaves would be utilized as food in these areas where algae and surf grass are so abundant.) Perhaps it is important for these individuals to hold on to any drift materials available to them. Figure 1 shows that there is a turnover rate of approximately 3 days for the nonfood items tested. This turnover of stones, shells, and leaves would ensure that these items are not "locked-in" and that algae or surf grass may replace them.

The primary adaptive function for the covering response in *S. purpuratus* is the capture of food items. Further observations on the ability of urchins to retain their cover during predation by *Pycnopodia* and displacement by wave action may shed some light on the role of covering in protection from *Anthopleura* predation.

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